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THE PROBLEM OF COLOR VISION

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THE problem of color vision is one of the most intricate which the biologist is asked to solve. The following paragraphs are intended to indicate the several methods which are being employed for its solution, together with some of the results thus far obtained. The anatomy of color vision will be considered first; then in turn its physiology and its development; and finally, the abnormal conditions of color blindness, together with the theories of normal vision to which they have given rise.

Anatomy. The mechanism of color vision is lodged in the rod and the cone cells. A ray of light, after passing through the lens of the eye and its vitreous body, penetrates several layers of the retina, thus arriving at the proximal ends of the elongated rod and cone cells. These cells are arranged in a single row. The light traverses the length of the cells to their distal ends which it stimulates. The rod and cone cells project against a single layer of heavily pigmented cells, the *stratum pigmenti retinae* (Fig. 1, S. P.). These have non-retractile processes which are found between the rods and the cones. The pigment fuscine, in the form of elongated or crystalloid granules, migrates into these processes when the eye is illuminated; in the dark it is withdrawn into the cell body.

Every rod cell consists of a rod, a rod fiber, and a nucleus, arranged as shown in Fig. 1, A. A rod, which is from 40 to 50 μ long and 1.5 to 2 μ in diameter, consists of a doubly refractive, lustrous *outer segment*, and a singly refractive, finely granular *inner segment*. In serum or dilute osmic acid the outer segment breaks into a series of regular transverse discs which are believed to indicate a stratified structure in the living rods. Visual purple is a pigment which occurs only in the outer segments of the rods.

It bleaches rapidly in the light, but (unless the pigmented stratum has been removed experimentally) it is soon restored in the dark. Light thus appears to incite chemical processes in the outer segments of the rods. The inner segments are sometimes described as having a longitudinally fibrillar structure in their outer portions. The opposite ends pass rather abruptly into the very slender rod fibers. Each fiber somewhere in its course expands to enclose the nucleus, and finally terminates in a pyriform enlargement. The nucleus in preserved specimens may have its chromatin arranged in a few broad transverse bands.

Every cone cell consists of a cone, a cone fiber, and a nucleus. The cones like the rods are divisible into outer and inner segments. The outer segment is usually shorter than that of the rod ($12\ \mu$) and tapers somewhat to its rounded extremity. It never contains visual purple, but otherwise, as for example in breaking into transverse discs, it resembles the outer segment of the rod. The inner cone segment bulges like the body of a flask. It is divided into an outer, longitudinally fibrillar, *ellipsoid* portion, and an inner contractile *myoid* portion. The non-contractile ellipsoid is said to become strongly eosinophilic in the dark. Because of the myoid substance the cones, unlike the rods, may alter their length. The contractility is said to be less in man than in the pig, and less in the latter than in some amphibia and fishes where the myoid segment is reported to shorten from $50\ \mu$ to $5\ \mu$. The nuclei are found in a mass of protoplasm near the base of the cone; beyond the nucleus the protoplasm forms a cone fiber which is thicker than that of a rod and which ends in a branched and expanded base.

The stimuli received by the outer segments of the rods and cones are transmitted through their fibers to the nerve cells of the retina, and thence to the brain. A single retinal nerve cell receives the stimuli from several rods and cones.

Since rods and cones are believed to have different relations to the perception of color their distribution in man and other animals should be significant. In the peripheral portion of the human retina rods are in excess, so that in sections three or four rods appear between every two cones. Near the depression or *fovea* where vision is most acute, rods and cones are equally abundant,

and in the fovea itself only cones are found. These cones, however, are strikingly rod-like in form, and greatly exceed the rods in length (Fig. 1, B). Slender cones are also found in the thickened *area centralis* which in many mammals replaces the human fovea.

In the ape, horse, pig, cow, sheep, and dog the rods and cones are similar to those of man. In rodents which avoid the light the cones are "very small and hard to detect since their inner segments scarcely differ from those of the rods, from which they may be distinguished by their much shorter outer segment. M.

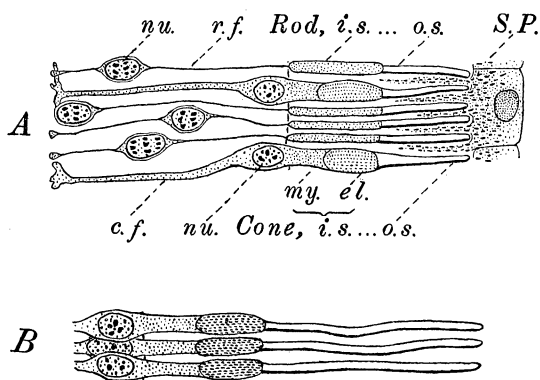


FIG. 1.— A, diagram of human rod cells and cone cells from the equatorial part of the retina. B, cone cells from the fovea, drawn on the same scale.

Schultze at first questioned the existence of cones in the mouse, guinea pig, mole, hedgehog, and bat. The cat undoubtedly has cones but they are small, slender, and except in the *area*, infrequent."¹ Birds have a single or double fovea, like that of man. Cones are small but very numerous, and in their inner segments they often contain a drop of oily substance, either colorless or various shades of yellow, green or red. Presumably these drops which are absent from the rods and some of the cones, exert an important influence upon color perception. In owls the bright colored drops are lacking and the cones are said to be fewer. Some reptiles have foveæ; two kinds of visual cells are reported, neither of which resembles the mammalian rods. M. Schultze

¹ The quotation, and much of this account of the retina, is from von Ebner's resumé in Koelliker's *Handbuch der Gewebelehre*, 1902, vol. 3, p. 818-832.

believed that reptiles have only cones. In fishes and amphibia, both rods and cones occur; in some sharks, rays, and eels, however, the cones so resemble rods that they may be overlooked. Whether or not deep sea fishes are without cones is apparently unknown. In the various groups of animals the rods and the cones each present modifications of structure, with which as yet physiological observations have not been correlated.

Physiology. The physiology of color vision is the study of the functions of the rod and the cone cells. In passing from a bright to a very dim illumination one experiences a momentary blindness; after becoming accustomed to the darkness, a modified form of vision is regained. In this *twilight vision* the fovea is far less sensitive to light than the more peripheral parts of the retina. Moreover all objects appear in shades of gray. The spectrum is bright but colorless, and its brightest part has shifted from the yellow portion toward the blue. Von Kries has explained these facts by assuming that the cones are the agents of day vision, and the rods of twilight vision.¹ Cones, exclusively, occur in the fovea where day vision is most acute; and rods predominate where twilight vision is at its best. The fluctuations in the visual purple of the rods show that they respond to the varying intensities of dim light, and this purple is known to desintegrate most rapidly in green light which appears brightest in twilight vision. Whether or not the bleached rods are active in day vision has not been determined.

It is probable that all cones do not respond to color stimuli. In the peripheral portion of the retina there is a partially color-blind region where red and green cannot be distinguished from one another; and the outermost portion of the retina is always totally color blind. Since cones occur in these areas they also must be color blind. From these considerations it is reasonably assumed that, in human vision, the ability to perceive colors depends upon the differentiation of certain of the cones.

Since at the present time the nature of vision cannot be determined by the microscopic examination of the retina, and since a very efficient vision may exist without color perception, it may

¹ Von Kries presents this *Duplizitätstheorie* in Nagel's *Handbuch der Physiologie*, 1904, vol. 3, p. 168-193.

fairly be questioned whether the lower animals are capable of color vision. The biological importance of this problem is very great, since prevalent theories of the development of the colors of flowers, and the bright plumage of male birds, assume a color perception in insects and female birds essentially like that in man. To learn what a bee actually sees has been thought impossible since it requires that one should possess the nervous system of an insect and still remain a man.

There is a large literature dealing with the distinctions which the lower animals make between various colors, but the factor of intensity or brightness has seldom been satisfactorily eliminated. The trout fisherman is confident that one fish, at least, discriminates colors with precision. Careful experiments with the chub, by feeding it from colored forceps and taking certain precautions to eliminate brightness, indicate that the chub distinguishes red from green and from blue.¹

Nagel, who is convinced that the phenomena of mimicry and warning colors demand color vision in animals, experimented with the dog. After taking precautions to eliminate brightness, he proved that the dog perceived the difference between red and blue, blue and green, and red and green.²

Kinnaman tested the monkey, *Macacus rhesus*. Its food was placed in one of six receptacles, precisely alike except that each was of a different color. When the monkey had learned to choose correctly the food-containing glass, a different color was selected. Thus the monkey learned to proceed at once to the receptacle with food, whether it was blue, yellow, red or green. It was tested also with a black and light gray glass. Having learned that the food was in the former, successively darker grays were substituted for the empty one. The percentage of wrong choices increased and it was found that grays were confused which the human eye can distinguish with perfect ease and certainty. Kinnaman concludes that "there can be no doubt that monkeys per-

¹ Washburn, M. F. and Bentley, I. M. The establishment of an association involving color discrimination in the creek chub. *Journ. of Comp. Neur.*, 1906, vol. 16, p. 113-125.

² Himstedt, F., and Nagel, W. Versuche über die Reizwirkung verschiedener Strahlarten auf Menschen- und Tieraugen, *Festschrift der Albert-Ludwigs-Universität in Freiburg*, 1902.

ceive colors." Two colors of equal brightness are distinguished better than two grays of equal brightness; and though the brightnesses are the same, colors may be distinguished from grays.¹

In the dancing mouse, however, the cones of which are at least very rod-like, Yerkes has recently found that color vision is extremely poor. There is some evidence of discrimination of red and green, and of red and blue, but none whatever of blue and green. Apparently such visual guidance as is received results from differences in brightness. The mouse discriminates blacks, grays, and whites.²

Because of the inherent difficulties in the investigation of color vision in the lower animals, comprehensive results have not yet been obtained, but the newer methods promise notable discoveries.

Development. Since color vision is a complex differentiation, it might be expected that in the course of development, an individual should successively pass through the simpler stages by which it was acquired. Anatomically it has been shown that the retinal layers first become distinct at the center of the retinal cup, and that the differentiation of the retinal cells decreases from the center toward the periphery. In the chick it is said that the cone nuclei may be identified at an earlier stage than the rod nuclei,³ but it is not generally recognized that one form of visual cell precedes the other.

The development of color vision has been theoretically considered by Mrs. Ladd Franklin.⁴ Her theory assumes that the colorless sensations, white, gray and black, are caused by a primitive photo-chemical substance called the gray substance, which is composed of numerous gray molecules.

These gray molecules, which persist in their primitive state only in the rods, upon disassociation furnish us with the gray sensa-

¹ Kinnaman, A. J. Mental life of two *Macacus rhesus* monkeys in captivity. *Amer. Journ. of Psych.*, 1902, vol. 13, p. 98-148.

² Yerkes, R. M. The sense of vision in the dancing mouse. *Journ. of Comp. Neur.*, 1907, vol. 17, p. 194.

³ Weyssse, A. W., and Burgess, W. S. Histogenesis of the retina. *Am. Nat.*, 1906, vol. 40, p. 611-634.

⁴ Franklin, C. L. On theories of light sensation. *Mind*, 1893, N. S. vol. 2, p. 473-489.

tions. In the cones the gray molecules have undergone a development such that a certain portion only of the molecule becomes disassociated by the action of light of a given color.

The differentiation of the primitive gray molecule is supposed to have taken place in three stages (Fig. 2). The first stage is

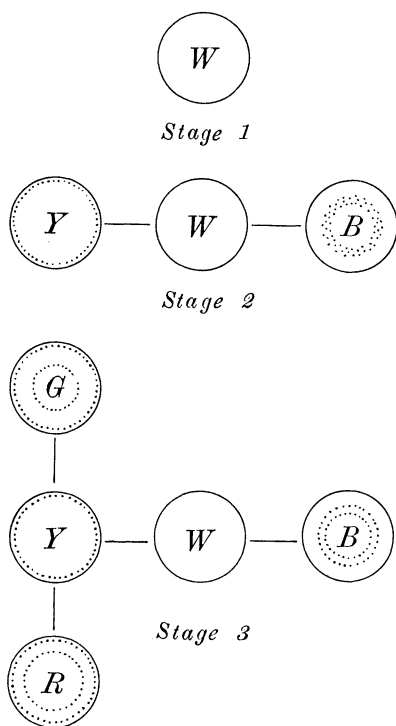


FIG. 2.—Diagram to illustrate the Franklin theory. The blue, green, and red groupings are represented by an outer, middle and inner circle of dots respectively. Disassociated groupings are omitted.

represented by the simple, primitive gray molecule, so constructed that it is disintegrated by light of any color, thus producing a gray or white sensation. In the second stage the molecule is more complex and contains two groupings, the disassociation of one of which gives the sensation of yellow and the disassociation of the other gives blue. The simultaneous disassociation of both gives white. This stage persists in the peripheral portion of the retina where neither green nor red can be perceived as such. In the third stage the yellow grouping is divided to form two new combinations, the disassociation of one of which produces the sensation of green and the other the sensation of red.

If the red and green groupings are disassociated together the resulting sensation is yellow; whereas the simultaneous disassociation of the red, green, and blue groupings produces the white sensation.

Schenck¹ has somewhat extended this theory by describing the development of the primitive gray molecule. Since in twilight

¹ Schenck, F. Über die physiologischen Grundlagen des Farbensinns. Sitz.-ber. d. Gesell. d. ges. Naturw. z. Marburg. 1907. Jahrg. 1906, p. 133-164.

vision the red end of the spectrum is lost, and the green-blue portion is its brightest part, he considers that the photo-chemical substance of the rods is attuned only to the green-blue light, which is perceived as colorless. Later this photo-chemical substance becomes sensitized in two stages, first to include the green-yellow, and then the yellow-red, which however are still perceived as colorless light. Thus a gray molecule like that of Mrs. Franklin's first stage is constructed. It occurs in the color blind peripheral cones. The formation of color-reacting groupings in the partly sensitized gray molecule leads, according to Schenck, to those forms of human vision in which the red end of the spectrum is shortened.

Observations upon the color perception of young children do not support these developmental theories. Holden and Bosse¹ tested two hundred children by placing before them square pieces of colored paper attached to a gray background of similar brightness. If the child made an effort to grasp the square, its color must have been perceived. It was found that the average child would react to all colors by the tenth month, the red end of the spectrum causing response a little earlier than the violet end. When ribbons of six spectral colors were placed before children of from seven to twenty-four months, red was selected first; orange or yellow second and third; and green, blue and violet last of all. Nagel² showed his child of twenty-eight months each of the spectral colors in varying degrees of brightness, at the same time teaching him their names. Red and green were learned easily, but blue was acquired with greater difficulty than any other color, including violet. Green, violet, and red were preferred; black, yellow, white, gray, and blue had secondary rank. Other experiments with the color perception of children have given different results. It is clear, however, that children are not known to pass from a color blind stage, through one of yellow-blue vision, to a discrimination of all the spectral colors. No race of men now exists in

¹ Holden, W. A. and Bosse, K. K. The order of development of color perception and color preference in the child. *Arch. of Ophth.*, 1900, vol. 29, p. 261-277.

² Nagel, W. A. Observations on the color sense of a child. *Journ. of Comp. Neur.*, 1906, vol. 16, p. 217-230.

which any of the colors is unknown; and the notion derived from studying the color terms and references in ancient literature, that man in historic times had a deficient color sense, is not substantiated. It may be that as in children, the red portion of the spectrum was preferred to the blue, but even this is not established.

Color blindness. All the colors which are normally perceived may be produced by combinations of the spectral red, green, and blue. Normal vision is therefore *trichromatic*. Sometimes in trichromatic vision the red end of the spectrum is shortened; in other cases a mixture of red and green, which to normal persons appears pure yellow, may seem tinged with red or green. Thus there are variations in trichromatic vision. Greater abnormalities may take the form of *dichromatic* and *monochromatic* vision. The latter is a rare pathological condition in which all colors are perceived as shades of one; vision therefore is essentially colorless (achromatic), the images obtained being comparable with photographs. In dichromatic vision color perception is so limited that all of the shades perceived may be made by combining two of the spectral colors red, green, and blue; blindness to the third of these colors may be partial or complete. The ordinary color blindness is dichromatic. Forty men and four women per thousand are either wholly unable to perceive certain colors or can recognize them only with difficulty. This defect is usually congenital and hereditary. It may cause so little trouble as to pass undetected until the age of seventy. All attempts to overcome the color blindness by educating the color sense in various ways, have failed.

Since dichromatic color blindness plays so large a part in the theories of normal vision, a portion of Dr. Pole's description of his own case is here inserted. He says,¹ "In the first place we see white and black and their intermediate gray, provided they are free from alloy with other colors, precisely as others do. (Such statements are confirmed by those who are color blind in one eye, the other being normal.) Secondly there are two colors, namely yellow and blue, which also if unalloyed we see, so far as can be ascertained, in the normal manner. But these two are the *only*

¹ Pole, W. Colour blindness in relation to the Homeric expressions for colour. *Nature*, 1878, vol. 18, p. 676-679.

colors of which we have any sensation. It may naturally be asked: Do we not see objects of other colors such as roses, grass, violets, oranges, and so on? The answer is that we do see all these things but that they do not give us the color sensation correctly belonging to them; their colors appear to us as varieties of the other color sensations which we are able to receive. Take for example the color red. A soldier's coat or a stick of sealing wax conveys to me a very positive sensation of color, by which I am perfectly able to identify, in a great number of instances, bodies of this hue. But when I examine more closely what I really see, I am obliged to conclude that it is simply a modification of one of my other sensations, namely yellow. It is in fact a yellow shaded with black or gray, a darkened yellow or yellow brown."

Dichromatic vision occurs in three forms, in two of which red and green are not differentiated from one another. The three forms are named *protanopia*, *deutanopia*, and *tritanopia* respectively. In *protanopia* the red end of the spectrum is shortened; that is, a portion which to the normal person is red, appears black. The remainder of the red, the orange, the yellow, and the green appear as successively lighter shades of yellow which, toward the blue, becomes gray or white. This white shades into blue which deepens toward the violet end of the spectrum. In *deutanopia*, which is the normal condition of a peripheral zone of the retina, the red of the spectrum is not shortened. Red, orange, yellow and green appear as lighter shades of one color, called red or yellow, and shade into a white or gray band which is a little nearer the red end of the spectrum than the corresponding band of *protanopia*. Blue is perceived normally. *Tritanopia* is a rare form in which yellow and blue are not recognized. The spectrum presents red and green portions, separated by a white band in place of the yellow. A dark green is seen in place of blue and the violet end of the spectrum is shortened.

Theories of Color Vision. Certain features of color blindness are ingeniously explained by Hering's theory, illustrated in figure 3. It is supposed that the cones contain a photo-chemical substance which is disassociated by red rays but which is built up by the green rays, giving rise respectively to the sensations of red and green. A second substance is broken down by yellow and built

up by blue light. As shown in the figure, orange is a mixed sensation due to the simultaneous partial destruction of the red-green and the yellow-blue substances. Yellowish green and greenish blue are likewise mixtures, and violet is supposed to combine the partial construction of the yellow-blue with the destruction of the red-green, the latter being indicated by the broken line. There are four pure sensations, red, yellow, green, and blue. Color blindness may be due to the absence or deficiency of the red-green substance (protanopia and deutanopia, the two forms being varieties of a single type), or to lack of the yellow-blue substance (tritanopia). Hering further considered that there was a white-black substance, built up in darkness to give rise to the sensation

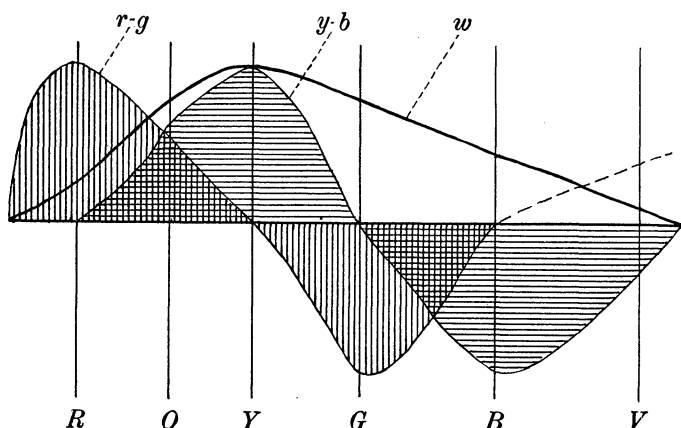


FIG. 3.—Diagram to illustrate Hering's theory of color vision. The red-green substance, *r-g*, is vertically shaded; and the yellow-blue substance, *y-b*, is transversely shaded.

of black, but destroyed in varying degree by different colored lights, thus giving white. In monochromatic vision the retina contains only this white-black substance. The curve *w* of figure 3 shows that the maximum stimulation of white is in the yellow portion of the spectrum. Without considering the difficulties concerning the white-black hypothesis, it may be questioned whether both constructive and destructive chemical processes can produce color sensations of similar nature. Mrs. Franklin considered that her theory was supported by the fact that the color sensations were all chemically destructive. Hering's theory, moreover, calls for four primary color sensations, whereas physi-

cists recognize that only three are necessary. Accordingly the physicist Young proposed a simpler theory antedating that of Hering. It was advocated by Helmholtz, and is generally known as the Young-Helmholtz theory.

According to the Young-Helmholtz theory there are three photochemical substances, red, green, and blue respectively, which are stimulated by the various rays of the spectrum as shown in figure 4. Absence of stimulation produces black, and the simultaneous disassociation of all three yields white. Protanopia is interpreted as red blindness, due to deficiency of the red perceiving substance. Deuteranopia is green blindness, and tritanopia is blue blindness. Since it would appear that the perception of white must be lost

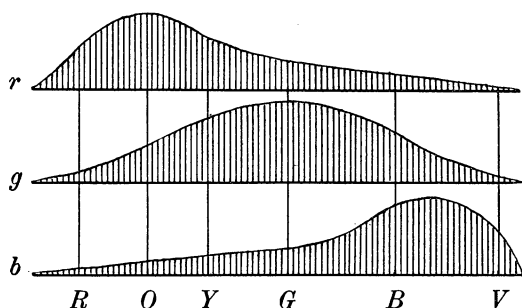


FIG. 4.— Diagram to illustrate the Young-Helmholtz theory. *r*, *g*, *b*, red, green, and blue perceiving substances, respectively.

with the disappearance of one of the three elements, the theory has been variously modified. In protanopia the red and the green substances may be so altered that each responds both to red and green light (Fick), or the red and the green substances may be imperfectly segregated, as assumed by Mrs. Franklin's theory. The close relation between the red and green substances is shown in Koenigs presentation of the Young-Helmholtz theory (Fig. 5). The absence of either would give rise to somewhat similar conditions, such as occur in protanopia and deuteranopia. The figure indicates that in trichromatic vision, the colors from yellow to blue affect all three substances to a certain extent, thus adding a small amount of white to the color sensation. In dichromatic vision the mixing of the two elements yields white. In case the red substance is absent, this white will appear nearer the blue than in case the green is absent; its position is indicated by the

intersection of the blue with the green and red curves respectively. In the absence of the blue substance, the white band is near the yellow. This accords with the observations upon the color blind. The absence of the green substance would not shorten the spectrum, but the lack of the red or blue would cut off their respective ends. All of these features are equally well explained if, instead of the absence of one of the three substances, such a modification of its reaction is assumed as would be illustrated by a lateral shifting of its curve in the diagram. Thus in red blindness the red curve is shifted to cover more closely the territory of the green; in green blindness the green is shifted toward the red; and in blue blindness the blue and green curves are brought together. Thus

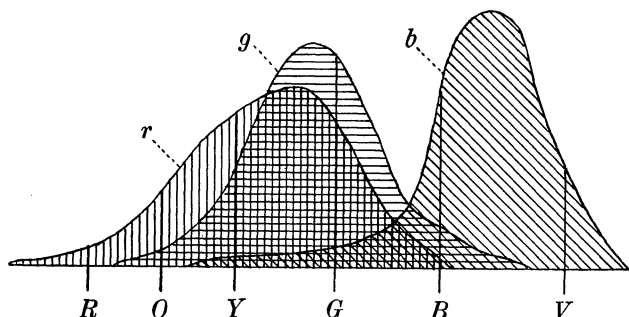


FIG. 5.— A modified diagram of the Young-Helmholtz theory, after Koenig.

in the color blind all three substances are present but in modified form. Since this modified Young-Helmholtz theory accords so well with observations on color blindness, it is generally considered as the most satisfactory explanation of color vision.

An interesting attempt has been made by Patten to bring this theory into relation with structural elements in the cones.¹ He believes that the visual cells of invertebrates are characterized by a fibrillation which is transverse to the direction of the incident light waves, and that the tendency of the vertebrate rods and cones to separate into transverse discs is evidence of a similar structure. Many hundreds of such fibrils may exist in a rod or cone. They are not supposed to vibrate like tense strings, but

¹ Patten, W. A basis for a theory of color vision. *Am. Nat.*, 1898, vol. 32, p. 833-837.

to act as 'conductors or resonators,' a fact which would not exclude chemical changes resulting in fatigue. The long fibrils respond to the red end of the spectrum and the short ones to the blue. In rods the fibers are of equal length and only monochromatic vision is possible, but in the cones their varying length allows a range of color perception. Any variation in the form or dimensions of

the cones would bring about corresponding changes in vision. The increased length of the cones at the fovea provides for a greater power of color discrimination. If the base of a cone were absent or cylindrical it would be red blind.

This theory is illustrated in figure 6. On the right is the diagram of a cone and its fibrils; the latter radiate from an axial filament, the existence of which has been discussed and denied by other investigators. The fibrils in the right half of the cone are drawn as responding to red, yellowish green, and violet light; the Young-Helmholtz curves are shown on the left. In nonpolarized light all of the fibrils in a transverse section of a cone respond uniformly, but in polarized light only such are effected as are

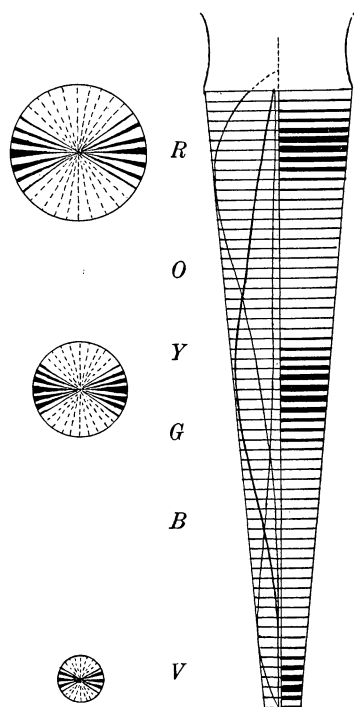


FIG. 6.—Diagram to illustrate the supposed fibrillar structure of human cones, and the way in which various light waves affect them. (Patten.)

indicated in the cross sections on the left of the figure. Thus the dullness of polarized light is explained. The correctness of this supposition, as Dr. Patten states, will be determined by extensive measurements, much more accurate and detailed than any heretofore made, of the visual elements in all classes of animals.

It will be noted that according to Patten's and Mrs. Franklin's theories the mechanism for reaction to all the colors may exist in a single cone. The Hering theory calls for the reaction to at least

two colors in one cone; but according to the Young-Helmholtz theory, although the three substances could exist in a single cone, each is declared to exist in a cone by itself. This is considered to be strongly in favor of the validity of the Young-Helmholtz theory. Since physiologists find no instance in which different sorts of impulses are conveyed over a given nerve fiber, it is believed that a single cone fiber can transmit only one sort of color sensation. The stimuli of the red, green, and blue cones respectively are supposed to be gathered by separate nerve cells of the retina, and the optic nerve consequently contains certain fibers transmitting only red, green, and blue sensations respectively. The mixing of the sensations, giving rise to the perception of shades and tints, is therefore accomplished in the brain and not in the cones. In an attempt to test this supposition, attention has been called to the perception of the colors of stars. The image of the star is so minute that it would cover but a single cone, but the conclusion that one cone perceives its color is invalidated by the fact that the retina is not sufficiently stationary; the image of the star falls in rapid succession upon several cones which may unite in giving the color perception. Those who believe in the specific energy of the rod and cone fibers dismiss at once several of the theories of color vision. It must be remembered, however, that the separation of the cones into forms responding to red, blue, and green light, with three corresponding sets of nerve cells and fibers to convey these separate stimuli to the brain, does not rest upon anatomical evidence.

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